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First reports of *Phylloporus gajari* from India

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Abstract—During macrofungal surveys in various tropical Sal-dominated (*Shorea robusta*) forests of West Bengal, we collected specimens of *Phylloporus*. After careful literature consultation, coupled with morphological examinations and molecular phylogenetic analyses with two genes, the species was found to be conspecific with *Phylloporus gajari*, which was originally described from tropical Sal forests of Bangladesh. We report *P. gajari* as a new record from India with detailed morphological description, illustration, 2-locus phylogenetic analyses, and extensive comparisons with related species.

Key words—*Boletaceae*, *Boletales*, *Dipterocarpaceae*, macrofungi, taxonomy

Introduction

Phylloporus Quél. is a species-rich genus in *Boletaceae* and it is evident from earlier studies that tropical to subtropical regions are biodiversity hotspots for this genus (Corner 1970, 1974; Singer & Gómez 1984, Heinemann & Rammeloo 1987, Singer & al. 1990, Neves & Halling 2010, Neves & al. 2012, Zeng & al. 2013, Hosen & Li 2015, 2017). *Phylloporus* encompasses a group of species with predominantly lamellate instead of poroid hymenophore (Singer 1986; Neves

& Halling 2010; Neves & al. 2012). Approximately 95 named taxa in this genus have been reported worldwide (https://www.indexfungorum.com) excluding subspecies and varieties. Due to phenotypic plasticity, morphological species recognition in this genus is quite difficult. Neves & al. (2012) and Zeng & al. (2013) have generated molecular phylogenies studies based on multi-locus DNA sequence analyses to elaborate species delimitation and biogeographic relationships of *Phylloporus*.

Many ectomycorrhizal fungi inhabit tropical Sal-forests (*Shorea robusta*) in India (Dutta & al. 2015, Ghosh & al. 2022a,b; Hembrom & al. 2017, Khatua & al. 2015, 2017, 2021; Paloi & Acharya 2019, Verma & al. 2018), but the diversity of boletes is unfortunately poorly understood. Only few species of boletes have been reported from these forests (Parihar & al. 2014, 2018a,b; Chakraborty & al. 2022). Recently, we have collected several basidiomata of a *Phylloporus* species during our macrofungal surveys to *Shorea robusta*-dominated forests in West Bengal. Significant macro- and micromorphological features combined with phylogenetic studies based on nrITS and nrLSU sequences revealed our specimen to be *Phylloporus gajari*, which was originally described from Bangladesh.

Here, we report the first occurrence of *P. gajari* from India based on a detailed morphological description and a combined (nrITS + nrLSU) phylogenetic inference.

Materials & methods

Morphological analysis

Fresh young to mature basidiomata were collected during field surveys to various areas of West Bengal during the rainy season (July and August), in 2020–22. Macromorphological characters were recorded in the field or at basecamp from fresh and dissected fruitbodies. Photographs were taken in the field with a Canon Power Shot SX 50 HS camera. Color codes and terms mostly follow Kornerup & Wanscher (1978). Samples were dried in a field drier. Micromorphological characters were observed from free hand sections of dried materials mounted in a solution of 5% KOH, 1% Phloxin, and 1% ammoniacal Congo red with an Olympus CX 41 compound microscope. Drawings of the anatomical features were made with a drawing tube at 1000× magnification. Microscopic photographs were taken with an Olympus BX 53 camera. The basidiospores were measured in lateral view. Basidiospores were examined in Melzer's reagent and measured in side view, excluding ornamentations. These measurements are represented as: (MIN–)AV-SD–AV–AV+SD(–MAX) spore-length × (MIN–)AV-SD–AV–AV+SD(–MAX) spore-width and Q=(MIN–)AV-SD–AV–AV+SD(–MAX), in which MIN= the minimum value, MAX= the maximum value, AV = AVERAGE value of total measured collections, SD = standard deviation and

Q = corresponds to basidiospore 'length/width ratio'. Statistics of other microscopic characters are expressed as the mean ± standard deviation with extreme values in parentheses. Basidium length excludes the length of sterigmata. Scanning Electron Microscope (SEM) images of basidiospores were obtained from dry spores that were directly mounted on a double-sided adhesive tape pasted on a metallic specimen-stub and then scanned with silver coating to observe patterns of spore-ornamentation at different magnifications in high vacuum mode (20 KV). SEM study was carried out with a Zeiss Evo 18 special edition model imported from Germany and installed at USIC Dept., Hemvati Nandan Bahuguna Garhwal University (HNBGU) Srinagar (Garhwal) India. The specimens are conserved in the Central National Herbarium, Botanical Survey of India, Howrah, India (CAL).

DNA extraction, PCR amplification and sequencing

Genomic DNA was extracted from 100 mg of dried basidiomata with the InstaGeneTM Matrix Genomic DNA isolation kit (Biorad, USA) following the manufacturer's instructions. Two nuclear markers were amplified: (1) the internal transcribed spacer region of ribosomal DNA (ITS), comprising the ITS1 and ITS2 spacer regions and the ribosomal gene 5.8S, using primers ITS1-F and ITS4 (White & al. 1990; Gardes & Bruns 1993); (2) a part of the ribosomal large subunit 28S region (LSU), using primers LR0R and LR5 (Vilgalys & Hester 1990). PCR amplification was performed on a thermal cycler (Eppendorf, Germany) programmed for 5 min at 95°C, 30 cycles of 1 min at 95°C, 30 s at 52°C, 2 min at 72°C, and a final 7 min extension step at 72°C. The PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN, Germany). Both strands of the PCR fragment were sequenced on the 3730xl DNA Analyzer (Applied Biosystems, USA) using the amplifying primers. The sequence quality was checked using Sequence Scanner Software v. 1 (Applied Biosystems). Sequence alignment and required editing of the obtained sequences were carried out using Geneious v. 5.1 (Drummond & al. 2010). The newly generated sequences in this study were submitted to GenBank (http://www.ncbi.nlm.nih.gov/Genbank/). Accession numbers of species used in the phylogenetic analyses are listed in Table 1.

Sequence alignment and phylogenetic analysis

The newly generated nrITS and nrLSU sequences of *Phylloporus gajari* (CAL 1903 and CAL 1904) from India and their close relatives were retrieved from the nBLAST searches against GenBank (https://www.ncbi.nlm.nih.gov/genbank), and relevant published phylogenies (Hosen & Li 2015, 2017; Zeng & al. 2013). Two datasets (ITS and LSU) were created separately. Both the datasets were aligned separately using the online version of MAFFT v. 7 with the L-INS-i strategy (Katoh & al. 2019) and then trailing ends of the alignment trimmed manually with MEGA v. 7 (Kumar et al. 2016). To eliminate ambiguous positions in the alignment as objectively as possible, Gblocks 0.91b (Talavera & Castresana 2007) was used. The program was run with settings allowing for smaller blocks, gaps within these blocks and less strict flanking positions. Species delimitation was first examined using single locus phylogenies.

Table 1. *Phylloporus* and *Xerocomus* species and sequences used in the phylogenetic analyses. New sequences are set in bold font.

Species	Voucher	Country	GenBank accession no.	
			ITS	LSU
P. alborufus	MAN022	Costa Rica	JQ003624	JQ00367
P. attenuatus	HKAS 76167	Bangladesh	KR094776	KR094780
	HKAS 76168	Bangladesh	KR094777	KR094781
P. bellus	HKAS 42850	China	JQ967240	JQ967197
P. bogoriensis	DED7785	Indonesia	JQ003625	JQ003680
P. brunneiceps	HKAS 59551	China	JQ967242	JQ967199
P. caballeroi	REH7906	Panama	JQ003638	JQ003662
P. castanopsidis	MAN104	Thailand	JQ003642	JQ003689
P. catenulatus	HKAS 76156	Bangladesh	KR094774	KR094778
	HKAS 76157	Bangladesh	KR094775	KR094779
P. cyanescens	REH8681	Australia	JQ003621	JQ003684
P. dimorphus	MAN128	Thailand	JQ003648	JQ003697
P. foliiporus	JLM1677	USA	JQ003641	JQ003687
P. gajari	**AG 20-003**	**India**	**OP550185**	**OP550198**
	AG 22-001	**India**	**OP550186**	**OP550196**
	HKAS 76158	Bangladesh	KR231696	KR231697
	HKAS 76159	China	KP780416	KP780420
	HKAS 76161	Bangladesh	KP780417	KP780421
	HKAS 76166	Bangladesh	KP780418	KP780422
	HKAS 81585	Bangladesh	KP780419	KP780423
	OR1104	Thailand	MT880254	—
	PHY	Thailand	MN580130	—
P. imbricatus	HKAS 54647	China	JQ967245	JQ967202
P. leucomycelinus	MB00-43	Panama	JQ003628	JQ003677
P. orientalis	REH8755	Australia	JQ003651	JQ003701

Species	Voucher	Country	GenBank accession no.	
			ITS	LSU
P. pachycystidiatus	HKAS 54540	China	JQ967254	JQ967211
P. pelletieri	Q7199c	Slovakia	JQ003639	JQ003668
P. rhodoxanthus	JLM1808	USA	JQ003654	JQ003688
P. rubeolus	HKAS 52573	China	JQ967259	JQ967216
P. rubiginosus	MAN117	Thailand	JQ003645	JQ003692
P. rubrosquamosus	HKAS 54542	China	JQ967260	JQ967217
P. rufescens	HKAS 59722	China	JQ967263	JQ967220
P. scabripes	REH8531	Belize	JQ003623	JQ003683
P. species	HKAS 74679	China	JQ967271	JQ967228
	HKAS 74680	China	JQ967272	JQ967229
	HKAS 74682	China	JQ967273	JQ967230
	HKAS 74684	China	JQ967275	JQ967232
	HKAS 74685	China	JQ967276	JQ967233
	HKAS 74687	China	JQ967278	JQ967235
	HKAS 74688	China	JQ967279	JQ967236
	HKAS 74689	China	JQ967280	JQ967237
	REH8729	Australia	JQ003650	JQ003699
P. yunnanensis	HKAS 52225	China	JQ967265	JQ967222
X. magniporus	HKAS 59820	China	JQ678697	JQ678699
X. subtomentosus	K 167686	England	JQ967281	JQ967238

When significant conflict was not observed among the single locus phylogenies, we concatenated all single locus alignments into one multi-locus dataset using BioEdit v. 7.2 (Hall 1999). The concatenated dataset was then phylogenetically analyzed using the maximum likelihood (ML) and Bayesian inference (BI) methods. For ML analysis, the concatenated alignment was carried out using raxmlGUI v. 2.0 (Edler & al. 2021) with GTRGAMMA substitution model. ML analysis was executed applying the rapid bootstrap algorithm with 1000 replicates to obtain nodal support values. For BI, the combined dataset was divided into two partitions: ITS and LSU. PartitionFinder2

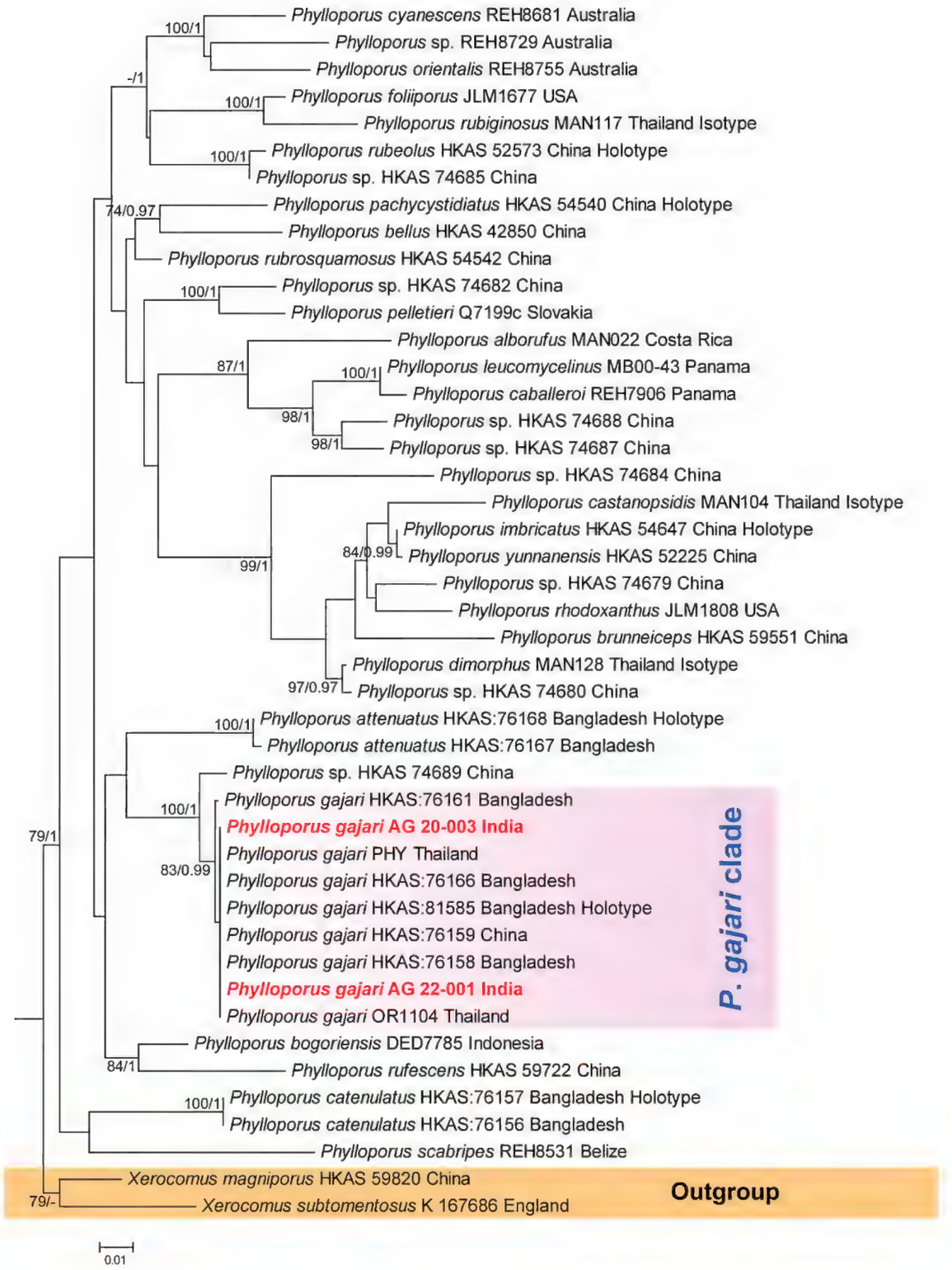

Fig. 1. Phylogram generated by Maximum likelihood analysis based on combined sequence data of nrITS and nrLSU for *Phylloporus gajari* and allied species. Maximum likelihood bootstrap support ≥70% are shown on the left of "/" and Bayesian posterior probabilities ≥0.95 are shown on the right, above or below the branches at nodes.

was used to find the substitution models for each partition (SYM+I+G for ITS, and GTR+I+G for 28S) using the Akaike information criterion (AICc) with a greedy search over all models (Lanfear & al. 2017). BI was computed in MrBayes v. 3.2.6 (Ronquist & al. 2012) with four Markov chain Monte Carlo (MCMC) chains for 1,000,000 iterations until the standard deviation of split frequencies reached below the 0.01 threshold. Trees were sampled every 100th generation. The first 25% of trees were discarded as burn-in. Chain convergence was determined using Tracer 1.5 (http://tree.bio.ed.ac.uk/software/tracer/) to ensure sufficiently large effective sample size (ESS) values (>200). Gaps in the alignment were treated as missing data in phylogenetic analyses. Maximum-likelihood bootstrap (MLbs) ≥70% and Bayesian posterior-probabilities (BPP) ≥0.95 are shown in the phylogenetic tree. *Xerocomus subtomentosus* (L.) Quél. and *X. magniporus* M. Zang & R.H. Petersen were used as the outgroup taxa for phylogenetic analyses.

Phylogeny

Both ML and BI analyses produced the same topology; therefore, only the maximum likelihood tree with both MLbs and BPP values are shown (Fig. 1). The nrITS data matrix contained 45 sequences and the alignment comprised 429 characters. The nrLSU data matrix contained 43 sequences and the alignment comprised 852 characters. The final combined dataset (nrITS + nrLSU) contained 45 sequences including our consensus sequences. The final alignment comprised 1281 characters including gaps.

Our combined 2-locus phylogenetic analyses show that sequences derived from our Indian collections nested (with robust support; MLbs = 83%, BPP = 0.99) within the clade consisting of seven *P. gajari* collections from Bangladesh, China, and Thailand. Our phylogenetic analyses strongly suggest that out Indian collections are conspecific with Asian *P. gajari*.

Taxonomy

Phylloporus gajari Hosen & Zhu L. Yang, Mycoscience 56(5): 585. 2015 Figs 2, 3

Basidiomata epigeous, small to medium-sized. Pileus 22–60 mm broad, convex to plano-convex when young, becoming applanate, depressed to broadly depressed at center and infundibuliform with age; margin plane to uplifted with age, entire; surface dry, smooth at first, then becoming rough to areolate and subtomentose to squamulose, reddish brown (8D–E4–7) to brownish red (10D4–7) when young becoming pale yellow (3A4), yellowish brown to pale yellow-brown (5D–E5–7) at maturity. Pileus context up to 7 mm thick at center, thinning towards the margin, pale yellow to yellowish white (3A2–3), turning greenish blue (24A–C6–8) when cut or bruised. Lamellae up to 5 mm

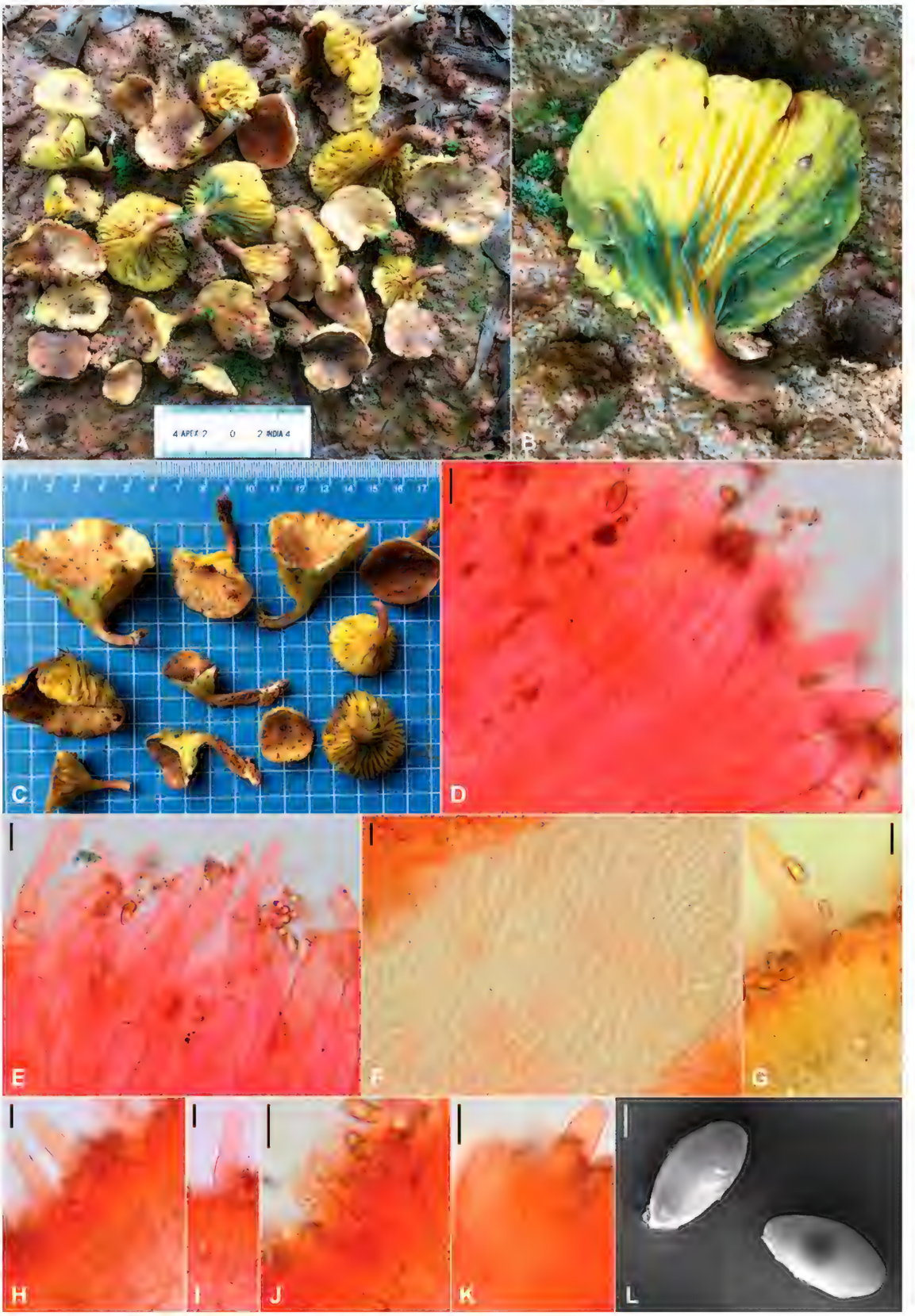

Fig. 2. *Phylloporus gajari* (CAL 1903; CAL 1904). A–C. Fresh and dissected basidiomes in the field and basecamp; D, E. Transverse section through pileipellis; F. Hymenophoral trama; G–I. Pleurocystidia; J. Basidia; K. Cheilocystidia; L. SEM image of basidiospores. Scale bars: D, E = 10 µm; F = 20 µm; G–K = 10 µm; L = 2 µm.

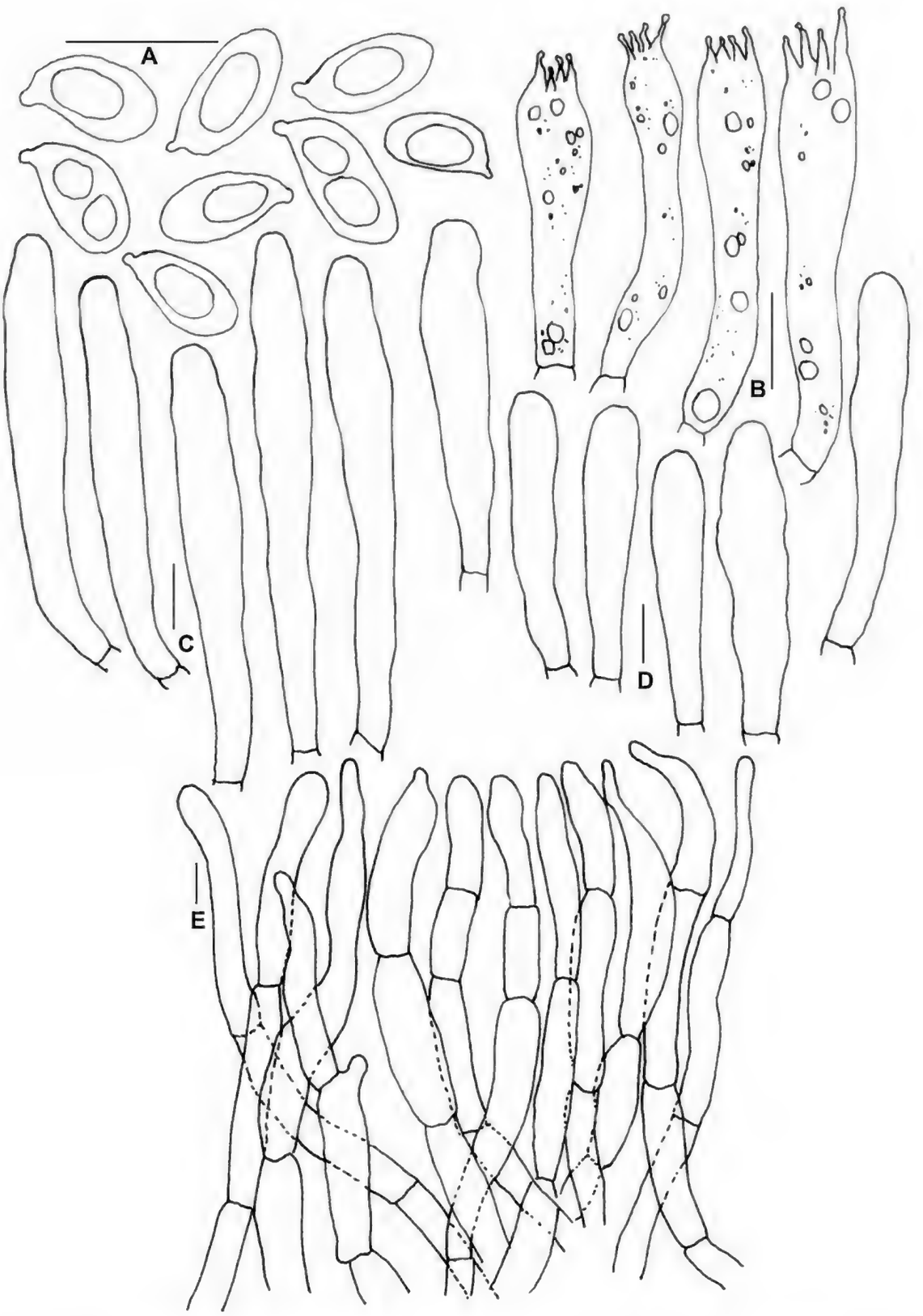

FIG. 3. *Phylloporus gajari* (CAL 1903; CAL 1904). A. Basidiospores; B. Basidia; C. Pleurocystidia; D. Cheilocystidia; E. Pileipellis. Scale bars: A–E = 10 μm.

deep, distant to subdistant (4–6/cm at pileus margin), pastel yellow, light yellow to yellow (2–3A4–7) with reddish brown spots, moderately thick, turning greenish blue (24A–C6–8) when cut or bruised; forked near stipe apex, midway to the margin, or near the margin; lamellulae present in different lengths; edges entire and concolorous. Stipe 20–55 × 5–8 mm, central, straight to curved, cylindrical; surface dry, very fine squamulose, brownish red to reddish brown (9C–E6–8). Stipe context solid, becoming stuffed with age, pale yellow (3A2–3); turning blue slowly in the upper part but usually unchanging in the lower half on exposure. Basal mycelium white.

Basidiospores (7.0–)8.1–9.1–10.2(–11.0) × (3.5–)3.9–4.2–4.6(–5.0) µm, Q = (1.67–)1.9–2.16–2.41(–2.63), subcylindrical, wall up to 0.5 µm thick, appearing smooth under light microscope but with bacillate ornamentation under scanning electron-microscope (SEM), inamyloid, pale yellow to yellow when observed in KOH and H_2O. Basidia 25–45 × 6–9 µm, cylindrical to subclavate, thin-walled, mostly 4-spored, sterigmata up to 6 µm long. Pleurocystidia 62–90 × 8.5–13 µm, subclavate to narrowly clavate with obtuse-rounded apex, thin-walled, colorless in KOH and H_2O. Lamellar edge fertile with basidia and cheilocystidia. Cheilocystidia 46–64 × 8–12 µm, with the same shape as pleurocystidia. Hymenophoral trama *phylloporus*-type. Pileipellis palisadoderm, composed of parallel to subparallel hyphal cells; terminal elements thin-walled, composed of chains of 4–5 cells, sometimes branched, 31–61 × 5–11 µm, mainly cylindrical or sometimes narrow at the apex, apically obtuse-rounded, colorless in KOH and H_2O. Caulocystidia 24–45 × 8–14 µm, ventricose to subclavate with obtuse-rounded apex, thin-walled, colorless in KOH and H_2O. Clamp-connections absent in all tissues.

Ecology & Distribution—occurring under *Shorea robusta* in tropical deciduous forests; known from India, Bangladesh, China, and Thailand.

Specimens Examined—**INDIA. West Bengal: Bankura district**, Joypur forest, alt. 73 m, on soil under *Shorea robusta* Roth (*Dipterocarpaceae*), 8 Jul 2020, A. Ghosh & M.E. Hembrom AG 20-003 (CAL 1903; GenBank OP550185, OP550198); **Jhargram district**, Lodhasuli, alt. 80 m, on soil under *S. robusta*, 14 Aug 2022, A. Ghosh AG 22-001 (CAL 1904; GenBank OP550186, OP550196).

Discussion

A combination of macro- and micromorphological characters such as small to medium-sized basidiomata with areolate to sub-tomentose, reddish brown to brownish red pileus, yellowish decurrent lamellate hymenophore staining greenish blue when cut or bruised, white basal mycelium, palisadoderm structure of pileipellis and stipitipellis, occurrence under *Shorea robusta* and

2-locus (nrITS and nrLSU) phylogenetic analyses undoubtedly confirm the Indian collections as conspecific to *Phylloporus gajari*. Morphologically, the Indian specimens are mostly corresponding to the holotype described from the neighboring Bangladesh (Hosen & Li 2015). However, the Indian specimens have comparatively smaller basidiospores (cf. 9–11 × 4–5 µm; Hosen & Li 2015) and show some branched hyphae in the pileipellis.

It is quite possible that *Phylloporus gajari* could be confused with *P. attenuatus* Hosen and *P. catenulatus* Hosen & T.H. Li in the field as they share similarly sized and colored basidiomata. However, *P. attenuatus* is distinguished from *P. gajari* by more crowded lamellae and attenuated stipe with pale red to yellowish brown surface (Hosen & Li 2017); and *P. catenulatus* differs from *P. gajari* in showing small basidiomata (20–40 mm diam), and subepithelium pileipellis composed of short chains of 3–4 inflated cells (Hosen & Li 2017).

Considering the size of basidiomata and stipe color, *P. gajari* can be confused with *Phylloporus rubeolus* N.K. Zeng & al. and *P. rubiginosus* M.A. Neves & Halling. However, *P. rubeolus* has an unchanging context when cut or injured, and an ectomycorrhizal association with *Lithocarpus* spp. (Zeng & al. 2013, Hosen & Li 2015). *Phylloporus rubiginosus*, originally described from northern Thailand, differs from *P. gajari* by having yellow basal mycelium, thick-walled hymenial cystidia, encrusted clavate or sinuous caulocystidia (Hosen & Li 2015). Another species, *P. bellus* (Massee) Corner, originally described from Singapore, macroscopically is closely related to *P. gajari* but has unchangeable to slightly cyanescent lamellae on bruising, pallid yellow stipe, and comparatively shorter and wider basidiospores (8.5–10 × 4.5–5.5 µm; Corner 1971).

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